On the Intestinal Canal of the Ichthyopsida, with especial reference to its Arterial Supply and the Appendix Digitiformis.

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(Plates I. & II.)

CONTENTS.

I. *On the Arteries of the Inferior Mesenteric Series, in the Ichthyopsida.*

The alimentary canal and its appended glands in the Plagiostome fishes receive their arterial supply from three or more trunks arising from the dorsal aorta (Plate I., *ao.*, fig. 1). Of these, the least variable are those which form the extreme anterior and posterior members of the series as hitherto described (*cf.* figs. 7, iii., iv., v.), viz. the so-called cœliac and inferior mesenteric arteries. In addition to these there are usually present two arteries which, unlike the rest, are paired, being derivative of the iliac vessels (*a.i.*, fig. 2); these, the paired nature of which has not before been detected*, pass directly backwards and inwards to reach the posterior wall of the cloaca, in a manner suggestive of the hypogastric arteries of the higher Vertebrata. The vessels alluded to above as "hitherto described" are so well known, and their courses and distribution have been so fully dealt with by Monro, Hyrtl, Parker, and others, that detailed reference to them here is unnecessary. The distribution of the

* Hyrtl has recorded the presence of one (*Raia clavata*) on the left side only (**18.** p. 30).

intervening arteries (the [anterior or superior] mesenteric, lieno-gastric, and anterior spermatico-mesenteric, of authors) * may for the present pass without further comment; the accompanying figures show them (*a.sm.*) to be variable in point of origin and in mutual relationship; not so, however, with the so-called inferior (posterior) mesenteric (*a.sm.* of fig. 1). That vessel invariably arises, in Batoids and Selachoids alike, some distance in advance of the processus digitiformis and so-called rectum (*dv''* and *i.l.* of fig. 1); it lies within the suspensory ligament of these structures and passes obliquely backwards and downwards, to reach the first named of them: on doing this it breaks up to form an elaborate system of vessels which are restricted to the appendix and to portions of the gut immediately adjacent (*cf.* fig. 1). In the long-bodied Selachoids this vessel usually supplies the above-mentioned parts alone; in some of them, however (ex. *Mustelus* [Parker, 27. p. 701]), as in the laterally extended Batoidei †, it sends branches to the genital glands, as is expressed in Parker's term "posterior spermatico-mesenteric" applied to it ‡. Be the branches and facts of distribution of this artery what they may §, its main trunk is invariably disposed as above described; it is primarily related to the posterior segment of the intestine with its appendage, and its most striking feature is its constant origin at a point remote from these anteriorly—consequent upon which it takes the said backward course.

I have recently published elsewhere || some observations in ichthyotomy that have extended over several years, in connection with which I have had occasion to inject a large number of Skate. While doing so, my attention became arrested by the occasional presence of one or more arteries passing from the dorsal aorta to the intestinal canal posteriorly to the region alluded to above, in addition to the paired vessels already described (*ante*, p. 381). The only mention of such vessels which I have been able to find is one by Hyrtl for the *Torpedo*, in which he

* *Cf.* Hyrtl (**18**), Parker (**27**), and Marshall and Hurst, 'Practical Zoology,' ed. 2 (London, 1888), pp. 234 *et seq.*

† *Cf.* fig. 1, *a. g.*, and Parker's 'Zootomy,' p. 62, fig. 20.

‡ 27. p. 701.

§ It distributes branches into the suspensory ligament which lodges it; and, from these, twigs may pass to the genital ducts, especially in the female.

|| Journ. of Anat. and Phys. vol. xxiv. (n. s. vol. iv.), pp. 407–422 (1890).

describes (18. p. 13) a single very small artery arising immediately in front of the crural vessels and becoming distributed to the cloaca—together with the hinder ends of the kidneys and related vasa deferentia.

Pl. I., fig. 1, represents the parts concerned in one of my specimens (*Raia clavata*, adult ♀), as dissected from the side after injection with French blue. The cloaca of these animals (*cl'*) becomes, as is well known, greatly modified—especially in the female—in relation to the genital ducts (*od.*); these approximate posteriorly in relation to a chamber (oviducal recess, *cl'''*) formed by partial subdivision of the cloaca. The arteries in question lay (*a.im.*) immediately in front of the approximated ends of the genital ducts; they arose between the kidneys, the anterior one leaving the aorta at about the middle of these organs *. These vessels lay, like the so-called posterior mesenteric (*a.sm.*), in the folds of the suspensory ligament of the so-called rectum; unlike that, however, they passed (not obliquely backwards but) directly downwards, at right angles to the long axis of the body. The distance between them was far less than that between the anterior one and the so-called posterior mesenteric. I have, in two instances, detected the passage from the extreme base of the aorta, immediately before the point of origin of the iliac vessels, of a couple of very delicate trunks for the post-cloacal wall (*a.im.*, fig. 1). Similar vessels may be present in *Acanthias*; they arise in the immediate vicinity of the bases of the kidneys, and reach the cloaca posteriorly to the genital ducts. I take them to be the homologues of that vessel referred to by Hyrtl in *Torpedo*. Neither set of arteries supplied (with the exception named above), so far as I was able to ascertain, anything but that portion of the intestinal canal immediately adjacent to its point of origin.

It is clear from the foregoing that any comparison which shall now or in future be instituted between the arteries of the posterior portion of the Skate's intestine and those of the corresponding parts in other Vertebrates must take into consideration

* In one specimen observed, the anterior renal artery of the exposed side arose at this point together with the intestinal vessel named, from a common trunk. I am indebted to my demonstrator, Mr. M. F. Woodward, for the knowledge of a specimen (*Raia maculata*, ♀) in which the posterior renal artery of either side gave off a vessel to the cloacal wall, a short distance behind the oviduct.

two sets of trunks—an anterior set (the so-called inferior [posterior] mesenteric) (*a.sm.*, fig. 1), arising in advance of the gut and passing obliquely backwards; and a posterior set, arising in the immediate vicinity of the gut and passing directly downwards. The alimentary tract of the higher Vertebrata receives its arterial supply from two sets of vessels—an anterior set (the cœliac and superior mesenteric arteries), which arise close together or from a common trunk; and a posterior (the inferior mesenteric artery or arteries), which arise far back and pass either directly downwards or but little obliquely backwards or forwards. These well-known facts at once suggest homology between the smaller vessels which I have herein described for the Skate (*a.im.* of fig. 1) and those of the inferior mesenteric series as ordinarily understood. The lack of oblique disposition is not, however, the only distinctive feature of these vessels. Those arteries known in the higher Vertebrata as the inferior mesenteric are so called from at least an analogy to the single vessel to which the term was first applied in mammals *. The inferior mesenteric artery of the Mammal supplies the rectum and the posterior section of the colon alone—it supplies, that is to say, the posterior portion of the large intestine; be this viscus relatively short (as in the Cat and Dog), or relatively long (as in the herbivorous mammals), the trunk of the inferior mesenteric artery never undergoes marked displacement either in a backward or forward direction. Such adaptive change as this vessel exhibits is of the nature of an extension of its branches along the dorsal wall of the gut, without displacement of its main trunk.

That the above remarks apply equally to most Amniota can be readily proved on appeal to the works of leading authorities. Among the Ichthyopsida, however, the recognition of a similar condition of the arterial supply has, to a great extent, escaped notice. To take a leading example, *i. e.* the Common Frog. In that animal, as is well known, the alimentary canal receives its arterial blood for the most part from a single cœliaco-mesenteric trunk; this supplies that viscus with its appendages from the post-œsophageal region to the middle of the large intestine (*cf.* Wiedersheim **8.** Abth. ii. pp. 76–77). There arises from the aorta, almost immediately in front of its point

* It is said to be absent in the *Didelphia* (Owen, **25.** p. 541) and *Monotremata* (Owen, **24.** p. 391); Hyrtl denies this (**17.** p. 7) for *Ornithorhynchus*.

of bifurcation, a well-marked vessel (*a.im.* fig. 4 *a*, *im.* iii. fig. 2), which passes directly downwards, or but little obliquely backwards, for distribution to the immediately adjacent wall of the large intestine. That viscus (*i.l.*) is in this animal, as in the Ichthyopsida generally, very short; and the vessel in question supplies its posterior half—supplies, that is to say, that portion of it which in the Mammalia becomes differentiated into at least the rectum; it has been termed by Wiedersheim, who first described it (**8.** Abth. ii. p. 77), the "*Arterie mesenterica inf. oder A. hæmorrhoidalis superior*," and by Marshall (**22.** p. 29) the "*hæmorrhoidal artery*." Inasmuch as it agrees, in every detail, with the inferior mesenteric artery of the Mammalia and higher Sauropsida (and especially with that of man to which the term "inferior mesenteric" was first applied), it must be similarly named *. An unfortunate confusion has arisen between its main trunk and the superior hæmorrhoidal artery of the higher Amniota, which is but a branch of its homologue; and the burden of proof that it represents this branch alone lies with those who have, as I believe, wrongly identified it.

Turning from the Frog to the Salamander, we find usually four such vessels represented (*a.im.*, fig. 5). These were first described by Hyrtl †, and subsequently by Rusconi (**30.** pl. vi. fig. 1), who confused them with the efferent veins of the cloaca; he, however, figured them with perfect accuracy, and they have been more recently diagrammatically represented by Wiedersheim (**33.** p. 715, fig. 550 B). Hyrtl has described in *Proteus*, *Siren* (*l. c.*), and *Cryptobranchus* (**19.** p. 109) a series of vessels having similar relationships. On examination, these arteries are seen (fig. 5, *a.im.*) to agree, in origin and distribution, with the inferior mesenteric artery of the Frog and of the Amniota on the one hand, and with at least the anterior two of the four vessels herein described for the Elasmobranchs on the other.

In all these animals individual variations affect, among other parts, the arteries under consideration; and, in the case of the Frog, the former have hitherto escaped notice. Fig. 3 combines the invariable condition met with in that animal (*a.im.* iii.)

* Wiedersheim figures it (*op. cit.* p. 77, fig. 37), in error, as distributed to the urinary bladder. I have never observed this arrangement. The allantoic bladder of the Amphibia receives its arterial supply, as does its homologue among the Amniota, from the iliac vessels.

† Cf. "*Lepidosiren paradoxa*," Prag, 1845, p. 39.

with such variations as I have from time to time observed (*a.im.* i. ii.). In one specimen (an adult ♀) there arose from the aorta, a short distance in advance of the artery (iii.) normally present, a single trunk (i.); this gave off, soon after its origin, a small branch to the oviduct of the left side, but its main trunk ran on to be distributed to the immediately adjacent wall of the large intestine. In two other examples (both males) I have noted the presence of two arteries (ii.) which, like the foregoing, passed at once to the adjacent intestinal wall; they differed from the last-named only in their relative slenderness, and in their exclusive restriction to the large intestine. The identity of these vessels with those of the Salamander is most striking, and when the parts under consideration in these animals and the fish are (as delineated in Pl. I. figs. 1, 3, and 5) reduced to the same size, the point of origin of the anterior of the series is seen to coincide throughout. Wiedersheim speaks of these vessels (33. p. 715) in the Salamander as arteries of the rectum ('Mastdarm'): in that they supply the greater portion of the large intestine, this term is insufficient—for, on the assumption (which can hardly be open to doubt) that the large intestines of the Amphibia and Amniota are homologous, they supply that section of the same which, in the ascending series of Vertebrata, becomes differentiated into the rectum and greater portion of the colon. Here the mind again reverts to the Mammal, and demands the declaration of homology between these vessels and the inferior mesenteric artery of it and of the higher Amniota, as the logical sequence to the facts.

The area of distribution of the single inferior mesenteric artery of the higher types being shown to coincide with that of the series in the Amphibia (and Thornback), the question immediately arises whether the condition of the first-named may not have arisen, either from a collecting together of the several trunks, or from atrophy of certain of the same, wholly or in part. The leading branches of these vessels usually lie, in the Salamander (fig. 5), along the dorsal middle line of the intestine; they there anastomose freely to form a generally well-defined longitudinal vessel, from which the side branches arise. In view of this, the obliteration of, say, the three anterior trunks of the series, between the aorta and the intestinal wall, would give us a condition identical with that of the higher types (cf. *ante*, p. 384); and it is conceivable that that realized in the latter may have arisen in

some such manner. I have met with individual Salamanders in which the arteries in question were reduced in number. The most striking example was one in which two, instead of four, main trunks were represented (fig. 6, *a.im.*); of these, the anterior one occupied the position and had the relationships of the anterior of the four more normally present, while the posterior one coincided in origin with the normal second artery, but partook of the distribution of the posterior three usually present (*cf.* fig. 5). These facts appear to me to indicate an origin of the single artery of the higher forms by concrescence such as I have postulated; and, in further support of a belief in the same, attention may be directed to the greater calibre of the posterior of the two arteries (fig. 6) in the Salamander*, and to an individual Frog (♀, fig. 4), in which the single artery present suddenly divided almost immediately after leaving the aorta (*ao.*).

II. *On the Arteries of the Cœliac and Superior Mesenteric Series, in the Ichthyopsida.*

I claim to have shown, in the foregoing, that those arteries which in the Ichthyopsida supply the posterior segment of the large intestine are serially homologous with the inferior mesenteric of the higher forms, and that the leading feature of these, taken collectively, is the invariable disposition of their main trunks at right angles to the axis of the body. In respect to this they contrast most forcibly with the great arteries which supply the rest of the alimentary canal; those generally arise far forwards, either from a single trunk (cœliaco-mesenteric) or from two (cœliac and superior [anterior] mesenteric) or more (cœliac, lieno-gastric, mesenteric, spermatico-mesenteric) trunks well known (*cf.* Hyrtl **18**, Parker **27**, and fig. 6, i. to v.).

The terminal portion of the intestine of the Plagiostome fishes is well known (*cf.* fig. 1) to be destitute of intestinal valve; it leaves the body in a straight line, becoming enlarged posteriorly to form the cloaca (*cl'*). To this valveless segment of the gut Monro applied (**23.** p. 94) the term "great gut," but that of "rectum" has been since more generally allotted it, apparently on a supposed homology with the rectum of the higher Vertebrata

* Wiedersheim figures an anastomosis between the third and fourth of the series (**33.** p. 715, pl. 550 B).

(*i. e.*, and more especially, of the Mammalia). Nearly all previous observers have agreed in regarding it either as a portion or the whole of the large intestine. It is characteristic of that part of the large intestine which, in the higher Vertebrata, lies immediately in front of that related to the inferior mesenteric vessels, that its nutrient arteries arise at a point remote from it anteriorly (*cf. ante*, p. 384); exceptions occur (ex. *Salamandra*, Pl. I. fig. 5), but, even in such, a wide interval is recognizable between the vessels in question and those of the inferior mesenteric series (*a.im.*). Either the posterior artery of this set (where more than two exist) or the most posterior branch thereof (where either one [*Rana*, most *Teleostei*] or two [*Raia*] exist) invariably supplies, in the higher Ichthyopsida and Reptilia *, the head of the large intestine, with a more or less considerable portion of the adjacent base of the ileum. That to which I here refer as the "head" of the large intestine includes so much of that viscus as is not supplied by the inferior mesenteric vessel or vessels (*i. e.* the short cæcum and that which in the Mammalia becomes the greater portion of the colon).

On turning to the Plagiostome fishes, a considerable variation becomes manifest (fig. 7, i. to v.) in the number and arrangement of these vessels. There are never more than three present, as ordinarily enumerated; four are indicated in the accompanying diagram (fig. 7, iii., iv., v.), but the terminal one of the series is usually excluded from the category, having been likened by Hyrtl, whose nomenclature has been hitherto everywhere adopted, to the inferior (posterior) mesenteric. As such this vessel is customarily described. Herein there lies a contradiction; for if it be true, as I claim to have shown (*ante*, p. 386), that the inferior mesenteric artery of the higher Vertebrata, with which it has been compared, is one of a series characterized, in all its variations, by the fact that its members do not arise at a point anteriorly remote from that portion of the gut which they supply, this vessel must be removed from that category, and the term "inferior mesenteric" will become inapplicable to it. Hyrtl's determination was based upon an examination of the vessels of

* *Cf.* Hoffmann, **14.** p. 1574. The term "inferior (posterior) mesenteric" has here been applied to that which clearly represents the vessel so named by Hyrtl in the Elasmobranchs, those which represent the inferior mesenterics of the Amniota and Amphibia being termed rectal arteries (*cf.* pl. cxxxv. fig. 1).

the *Batoidei*. On reference to fig. 7, ii., which represents the origins of these in the Thornback (*Raia clavata*), it will be seen that the cœliac (*a.c.*) and superior mesenteric, as ordinarily described, arise far forwards and close together, as in the majority of the higher Vertebrata, and that the so-called inferior mesenteric (the right of the two lettered *a.sm.*) arises far behind them, in a manner certainly suggestive of the mammal itself, and such as might appear, were it true of all Plagiostomes, to justify this comparison. In those Selachii of whose arteries we possess a sufficient knowledge, the cœliac and superior mesenteric arteries of the Batoids are represented by three trunks (fig. 7, iii. to v.—the cœliac ; superior, anterior, or anterior spermatico-mesenteric ; and the lieno-gastric, of authors). In *Acanthias* the two last named arise far back (v.), in close proximity to that which Hyrtl likened to the inferior mesenteric trunk.

Acanthias (fig. 7, v.) and *Raia* (ii.) represent the extreme terms in the Plagiostome series, so far as our knowledge of the arteries of their alimentary canal goes. The origins of the latter are indicated to scale in the accompanying figures, and it will be seen that there is a constancy of relationship between the cœliac and so-called inferior (posterior) mesenteric vessels—the latter shifts its position only in the Batoid, in which it is dragged forwards, as it were in sympathy with the superior mesenteric, which lies in close proximity to the cœliac *.

No competent anatomist would hesitate to relegate the cœliac and superior mesenteric arteries of *Raia* (fig. 7, ii.), as ordinarily described, to a common category ; nor would he, on first examination of *Acanthias* (fig. 7, v.), hesitate to similarly associate the two arteries of the superior mesenteric series † with that termed by Hyrtl and subsequent writers the "inferior mesenteric." Herein lies the whole difficulty—are we justified in longer referring, with Hyrtl, the vessel in question (*a.sm.* of fig. 1), to the inferior mesenteric series ?

In *Scyllium* (fig. 7, iv.) we meet with a condition essentially transitional between the two extremes above mentioned (*Raia* ii. and *Acanthias* v.), inasmuch as the superior mesenteric arteries

* I suspect that the changes incident upon the lateral extension of the body, with its attendant abbreviation from behind forwards, may be here active.

† I refer to these vessels as such for brevity, and in no want of respect for either the work or nomenclature of my contemporaries.

arise very nearly midway between the cœliac and Hyrtl's "posterior mesenteric." The dotted line α—β of the figure will testify to the truth of the assertion that, with respect to the origins of these arteries, a gradational series is forthcoming among easily accessible forms; and, on the knowledge of that which has gone before, we should be justified in removing the so-called "inferior" or "posterior" mesenteric artery of the Plagiostomes from that category, and relegating it to that of the superior mesenteric series.

The inferior mesenteric arteries of those Ichthyopsida least remote from the fishes (*i. e.* the *Urodela*) are usually four in number, and I have attempted to show (*ante*, p. 387) that the reduction in number of these vessels met with among the higher forms (ex. *Rana* 1 to 3, *Lacerta* 2 to 3, *higher Amniota* 1 or more) may, in all probability, have been due to modification of such a series by concrescence. In view of the variation of the cœliaco-superior-mesenteric arteries before referred to, one is led to ply the same question, viz.: may not they be the modified derivatives of a closely related series? That they are liable to concrescence at the present day cannot be doubted, since, in *Acanthias* (fig. 7, v.), it occasionally happens that the mesenteric and lieno-gastric trunks unite. Among the *Urodela* we meet with a condition of the arteries of the cœliaco-superior-mesenteric series in which (*Salamandra*, fig. 5) the several trunks lie (*a.cm.sm.*) closely aggregated side by side. The most recent account of these is that given by Wiedersheim (**33.** p. 175). Hyrtl has long ago described them, as also a similar series in *Proteus*, *Siren*, and *Cryptobranchus* (cf. *ante*, p. 385); Hoffmann alludes to them (**13.** pp. 493–494) as the arteriæ "gastrica anterior," "gastrica mesenterica," and "mesenterica primæ et accessoriæ." Wiedersheim figures, in *Salamandra*, six main trunks; I find seven to be the usual number * (fig. 5, *a.cm. sm.*). Be there six or seven present, the posterior one invariably supplies the head of the large intestine; in its relationships to the inferior mesenteric vessels it stands identical with the so-called hæmorrhoidal branch of the Frog's superior mesenteric on the one hand, and with the so-called inferior or posterior mesenteric of the Plagiostomes on the other. The arteries of this very interesting

* Hyrtl enumerates from 13 to 17 for the collective series in the Urodeles referred to.

Salamandrine series differ from the corresponding vessels of other Vertebrata only in the fact that their main trunks show but little signs of forward displacement. In that they leave the dorsal aorta nearly at right angles to the long axis of the body, they approximate towards the condition of the inferior mesenteric arteries (cf. *ante*, p. 388); there is, however, a very marked gap * between the two sets of vessels, and, of the two, the anterior are by far the most closely aggregated (*cf.* fig. 4). Fusion of these, more or less marked, would give us the varying conditions met with in the other Vertebrata. I have satisfied myself that reduction in their number, such as that figured by Wiedersheim (*loc. cit.*), results either from fusion of a couple of the anterior mesenteric trunks (*a.sm.*), or from confluence between the most anterior of these and the cœliaco-mesenteric artery (*a.cm.*). In this we have evidence of a process of change identical with that to which the facts concerning the inferior mesenteric vessels appear to point (cf. *ante*, p. 387); taken in conjunction with that above described in *Acanthias* (p. 390), it points unmistakably to the conclusion that the less numerous cœliac and superior mesenteric arteries of the other Vertebrata may have arisen (as I have attempted to show for the inferior mesenteric) from a more numerous series, by concrescence. If I am right in referring the posterior mesenteric artery of the Plagiostome fishes to this cœliaco-anterior-mesenteric series (and this, in the long run, is the leading conclusion for which I am contending, so far as the blood-vessels are concerned), Hyrtl's observation (**18.** p. 13), that in *Torpedo* it is represented by two arteries which proceed side by side to the processus digitiformis and adjacent parts, is very welcome; for it suggests that in that which I would term the supernumerary vessel we may, in all probability, be dealing with the representative of one which has been lost in the allied forms. The arteries of this series vary in number, in the Salamander, from seven to six; in the knowledge of the fact discovered by Hyrtl they do so, in the Plagiostomes, from five to three; and when it is seen that they are to-day showing signs of concrescence (cf. *ante*, p. 390), we are enabled to point to the existence of a gradational series which very strongly favours the conclusion that the vessels repre-

* This appears to have been exceptionally marked in the individual figured by Wiedersheim (**33.** fig. 550 B).

sentative of the same in the majority of living Vertebrates *may* have arisen, by concrescence, in a manner analogous to that of the allied inferior mesenteric set *. Moreover, the retention, among the tailed Amphibia, of that which would appear to be the lowest stage in the development of the intestinal arteries becomes the more interesting and suggestive in view of the lowly condition of the urinogenital organs of these animals †.

From the foregoing I would deduce the belief (i.) that the leading arteries of the alimentary canal of the Vertebrata may be resolved into two well-marked series—(*a*) that (including the cœliac, superior or anterior mesenteric, lieno-gastric, and spermatico-mesenteric arteries of authors, together with the so-called inferior or posterior mesenteric of the Plagiostomes) which I would propose to term the *anterior splanchnic series*; and (*b*) that embracing the inferior mesenteric arteries as herein defined (*ante*, p. 388), for which the term *posterior splanchnic series* may suffice: (ii.) that the two series of arteries are always separated by a more or less wide interval, which increases in proportion as each becomes modified by concrescence: and (iii.) that such modification, although common to the two series, affects the posterior one in the least marked degree ‡. The vessels of the anterior splanchnic series supply the alimentary canal and its appended glands from at least the base of the œsophagus to the head of the large intestine, where such can be definitely recognized; while those of the posterior series are invariably restricted to the posterior portion of the large intestine (colon in part and

* It is pertinent to remark here that examination of a series of individuals of our commonest Ichthyopsida will generally reveal facts of similar significance. In the *Gadidæ* it is the rule to find the cœliac and superior mesenteric arteries arising conjointly (*cf.* Johannes Müller's 'Myxinoiden,' Fortsetzg. 3, pl. iii. fig. 13, and Stannius's 'Anat. d. Wirbelth.,' Zweite Aufl. p. 245); but individuals in which they arise independently daily reach our laboratories (*cf.* Parker, 'Zootomy,' p. 113, fig. 32). Similarly, individuals of the common Frog occasionally present themselves in which an identical condition may be seen (*cf.* Huxley & Martin's 'Practical Elem. Biology,' revised ed. 1888, p. 87).

† *Cf.* Balfour, "On the origin and history of the Urinogenital Organs of Vertebrates," Journ. Anat. & Phys. vol. x. p. 28 (1876), and Jungersen [20], pp. 192 *et seq.*

‡ The facts obviously suggest a likeness to the metameric symmetry of the offshoots of the intestinal vessels of the segmented worms; but further speculation under this head would be now premature.

rectum, when differentiated, with the cloaca). The posterior series appear to be wanting only when (espec. *Teleostei, Marsupialia*) the anterior splanchnic ones supply the entire viscus. Whether this condition results from the suppression or absence of the posterior series, or from anastomosis between it and the anterior, there is, at present, no evidence to show. I have examined a large number of Teleostei, in vain, in the hope of finding, in that order, a more general development of the inferior mesenteric trunks, as defined by myself.

III. *On certain Appendages of the Intestinal Wall of the Ichthyopsida, in relation to their Arterial Supply.*

If the foregoing considerations are sound, it will follow that the so-called inferior mesenteric artery of the Plagiostomes (*a.sm.*, fig. 1) really represents that vessel (the posterior vessel of the anterior splanchnic series) which is normally distributed to the head of the large intestine with its adjacent parts, in the higher Vertebrata. If this be so, that which we, in the Plagiostome fishes, customarily regard as the rectum, would appear to represent the entire large intestine together with a portion of the small one, as defined for the terrestrial Vertebrata.

The most conspicuous structure present in this region of the Plagiostome's gut is the *processus digitiformis* * (*dv''*, fig. 1). On comparison with the Frog † (fig. 4) or with a Lizard ‡, this struc-

* Better known as the "rectal gland" ("bursa cloacæ" of Retzius). I prefer to exclude these terms from the text, for reasons which the sequel will show.

† That the Frog possesses a rudimentary cæcum is at once clear on comparison with a Lizard. If the head of the large intestine be opened from the side, as represented in fig. 3, it will be seen that the ileum enters that viscus from below; a line drawn vertically through the valvular extremity of the ileum will pass behind an overhanging enlargement of the antero-dorsal wall of the large intestine, and that this represents the cæcum coli is clear on consideration of the well-known facts of morphology of that structure.

The discovery of the Frog's cæcum has been attributed to myself, in error (Wiedersheim [**33**], p. 564). I was the first to figure it ('Atlas of Practic. Elem. Biology,' 1885, pl. 1. fig. 13); it was originally described by Huxley in Huxley and Martin's 'Elem. Biology,' original ed. p. 166 (1875).

‡ *Cf.* Parker, 'Zootomy,' p. 164 and fig. 40.

ture, when viewed in relation to the intestine on the one hand and the arteries on the other, is found to answer precisely to the appendix vermiformis of the Mammalia. Like that, it forms a glandular appendage to a diverticulum of the mid-dorsal intestinal wall; like that, it receives its arterial supply from the most posterior offshoot of the superior mesenteric artery. There is here raised the most revolutionary point in my investigation; and the suggestion would appear, at first sight, to be negatived by the mode of origin of the diverticulum in question in the Plagiostomes, from the middle instead of the anterior extremity of that which, in them, we are accustomed to regard as the rectum or large intestine. It must not be forgotten, however, that the application of the terms "rectum" and "colon" to the intestines of fishes implies only a conception of rude analogy to the parts so named in the Mammalia.

The appendix digitiformis consists of either a digitiform, as its name implies (Pl. II. figs. 8–14), or a slightly coiled structure (*Rhina*, fig. 15), which communicates with the gut by means of a more or less well-marked duct (*dv'*). It has been described in a general way by various observers for different genera and species*; but neither the gland nor its duct have thus far received the attention which they merit. That the gland arises as a diverticulum of the intestinal wall is clear from the researches of Blanchard (2) †. The intestinal spiral valve of the Plagiostomes usually terminates at a point remote from the origin of this appendix digitiformis and its duct (ex. *Raia*, fig. 1, *v.i.*). Parker has recorded (26) for the valve, in this and other Elasmobranchs, an astonishing range of individual variation in its mode of disposition and total area; he has failed, however, to lay sufficient stress upon the striking nature of the same in relation to its point of termination posteriorly. In the adult Skate, for example, it may either terminate at a point much farther forwards than that represented in fig. 1 (*cf.* Parker, *l. c.* pl. 10. figs. 1 & 8), or at that marked * in the same, thus diminishing the distance between its posterior extremity and the orifice of the duct of the appendix digitiformis. In *Notidanus* (*Heptanchus*) the valve extends still further back, and terminates, in a slightly interrupted but exceedingly definite manner (fig. 14, *v.i.*), immediately in front of the

* For *résumé* see Duméril (7), pp. 157, 158.

† My attention was first drawn to this paper by my friend Dr. Hans Gadow.

orifice just alluded to *; while in *Cestracion* it does so at a point situated lineally with this below.

That the spiral valve performs an absorptive function can hardly be doubted after the investigations of Edinger (9. p. 678) into its histological structure. That segment of the intestine which bears it comes thus to represent most nearly the ileum † of the higher Vertebrata; and, inasmuch as the valve may extend back to the point of origin of the "duct" of the appendix digitiformis (*dv'*, fig. 14), that portion of the gut lying immediately in front of the latter can consequently be most satisfactorily compared only with the small intestine. The application to it of the term "rectum" is no longer justifiable; and the above facts warrant the restriction of the term "large intestine" to so much of the gut as is situated behind the duct referred to (= that portion embraced by the lines radiating from *i.l.* in fig. 1). If this be admitted, the comparison, before instituted (*ante*, p. 394), between the appendix digitiformis and its duct and the appendix vermiformis and cæcum, becomes vastly strengthened, and these two sets of structures may justly be alike regarded as median diverticula of the antero-dorsal extremity of the large intestine.

Parker's researches show (26), when looked at critically, that the spiral valve varies, among Elasmobranchs generally, in nothing more conspicuously than in its degree of abbreviation from behind forwards. The belief in the primitive characters of the living *Notidanidæ* is becoming more and more justifiable from the researches of palæontologists ‡; and we may therefore attach a special importance to the great development of the spiral valve in *Heptanchus* (cf. *ante*), as it furnishes us with a condition from which, so far at any rate as backward extension

* Such does not appear to be the case in the allied *Chlamydoselache*. *Cf.* Garman (10) and Günther (11).

† Home alluded to it (15. p. 391) as the "jejunum." It is exceedingly unfortunate that in students' books current it should be spoken of as the "colon" (Marshall and Hurst's 'Junior Course in Practical Zoology,' ed. 2, 1888, p. 219).

‡ *Cf.* A. S. Woodward, P. Z. S. 1886, pp. 218–224, and Geol. Mag. dec. iii. pt. iii. 1886, pp. 205 *et seq.*

Haswell has still further emphasized the belief, in his proposal (Trans. Linn. Soc. N. S. W. vol. ix. pt. i. p. 44, 1884) to subdivide the Selachoidei, in accordance with the great diversities in their skeletal anatomy, into the two suborders of the *Palæoselachii* (*Notidanidæ*) and *Neoselachii*.

It is worthy of remark that the spiracular gill of these Sharks, although a

is concerned, there may be derived that met with in all other living *Plagiostomi*.

It remains now to consider, more closely than heretofore, the differences and resemblances between the appendix digitiformis and its "duct" and those structures to which the terms cæcum coli and appendix vermiformis have been applied. The appendix digitiformis lies to the left side of the valved intestine, as pointed out by Blanchard (2. p. 190)*, and its apex is, in the adult, usually directed towards the animal's right. Examination of it in relation to the lumen of the gut shows it to be, however, a derivative of the mid-dorsal intestinal wall. On opening the body-cavity from the ventral aspect in the Common Skate, the structure in question is seen to occupy the interspace between the pyloric sac of the stomach and the adjacent intestine, and to be disposed lineally with the former. Anteriorly it is received into a notch in the posterior border of the pancreas. Such may be the disposition of the cæcum among certain of the higher Vertebrata, and in *Rana* and *Lacerta* that organ, if examined with sufficient care, may generally be found to lie at or towards the side †.

The appendix digitiformis and its "duct" are, like the appendix vermiformis and cæcum coli, extremely variable in development in even allied forms ‡. Figs. 8 to 14 represent the former in

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"pseudobranch" as recently defined by Sagemahl (Morphol. Jahrb. t. x. 1885, p. 113), has just been shown by Virchow (Verhandl. d. physiol. Gesellsch. Berlin, 1889–90 [Archiv. f. Anat. u. Phys., Phys. Abth. 1890, pp. 170 and 178 *et seqq.*]) to differ from that of all other Chondrichthyes in having the essential structure and the capillary networks of a true demibranch; and it is difficult to believe, in view of his researches, that it can be other than respiratory in function.

* In *Læmargus* this is so markedly the case that the suspensory mesentery of the gland shifts its position, and becomes attached obliquely across the antero-dorsal moiety of the same.

† This fact would appear to account for the representation of the same as a diverticulum of the ventral wall of the gut (cf. *Rana* [Marshall, 22. p. 27, fig. 5] and *Amphisbæna* [Bedriaga, 1. pl. iv. fig. 2]).

‡ Blanchard has directed attention to this (2. p. 182) so far as the appendix digitiformis is concerned. He gives as the minimum length observed 0·8 centim. (*Chiloscyllium plagiosum*, length of body not stated). In a *C. ocellatum* of 46 centim., recently captured by my friend Prof. A. C. Hadden in the Torres Straits, and by him generously placed at my disposal, the gland measures 0·6 centim.

typical examples, drawn to the same scale relative to the transverse diameter of the base of the adjacent intestine (α—β of Pl. II. fig. 14). These structures show, so far as I have been able to ascertain, little sign of individual variation: the first noticeable features concerning them are (i.) that the length of the duct bears little or no proportion to either the length or bulk of the gland—the latter is most massive in *Læmargus* (*dv''*, fig. 10), where the duct (*dv'*) is shortest; and (ii.) that the maximum attenuation of the gland is not accompanied by that of the duct (cf. *Acanthias*, fig. 13, and *Notidanus*, fig. 14). This "duct" has been previously best described by Home* and Blanchard. The last-named author regards it (*Acanthias*, 2. p. 182) as a duplicature of the intestinal mucous membrane. It is more or less marked in all the *Selachoidei* which I have been able to examine; and it will be seen from the accompanying figures that it attains its greatest attenuation in *Notidanus* (fig. 14); between the conditions exemplified in this genus and in *Læmargus* (fig. 10), taken as extreme terms in the series, gradational types present themselves in *Scyllium*, *Cestracion*, and *Acanthias* (figs. 11, 12, 13). On examination of these, the duct in question (*dv'*) might readily appear to have been formed by a downward extension of a simple fold of the intestinal wall, such as that of *Læmargus* (fig. 10). *Læmargus* is remarkable for the possession of the most aberrant type of intestinal canal met with in living Plagiostomes. Its duodenal segment is, unlike that of all other Elasmobranchs, tubular and flexed, and the bearer of a couple of enormous diverticula which Turner has (31. p. 245) compared to the pyloric cæca of the *Osteichthyes*; its appendix digitiformis (fig. 10) is the most massive that has yet been observed; and, in view of the facts just named, it becomes doubtful whether that structure may not be in a much modified condition.

In the *Batoidei* the processus digitiformis communicates with the intestine by a short non-constricted passage (*dv'*, fig. 1), little suggestive of the "duct" of the Selachoids. Monro has already figured this in *Raia*†, and I find an identical condition in *Torpedo*, *Trygon*, and the rare *Hypnos subnigrum*. Comparison of figs. 1 and 3 at once suggests an homology between

* He naïvely likened the apparatus (15. p. 392 [A. D. 1814]) "to the ink-bag in the Cuttle-fishes" (*cf.* his 16. pl. xcviii.).

† 23. pl. ix. fig. 2.

this passage (which is in reality a wide funnel-shaped prolongation of the gut) and the cæcum coli of the higher Vertebrata. Comparison of Pl. II. figs. 9 to 14 shows unmistakably that that prolongation (be its original significance what it may) has become converted by constriction into the "duct" of the processus digitiformis of the Sharks; and suggests that the *Batoidei* in all probability retain a more primitive condition thereof than do the *Selachoidei* of to-day. Attenuation of the "duct" has been seen (*ante*, p. 397) to be most marked in *Notidanus* (*dv'*, fig. 14). Thanks to the generosity of Prof. Huxley, I have been enabled to examine a fœtal *Notidanus** measuring 15 centim. in total length. In it the duct is much shorter and relatively wider than in the adult, and in no way bound down to the intestinal wall; it stands out from this in the manner indicated in fig. 8 (*Zygæna malleus*). In *Zygæna* this condition is retained; and it will be observed that it is just such as would result from elongation of the intestinal diverticulum of *Raia* (fig. 9) with accompanying constriction. *Squatina* ([*Rhina*], fig. 15) is, in respect to this constriction, transitional between *Raia* and *Zygæna*. That the *Selachoidei*, in which this structure becomes most modified, pass through a stage such as is here represented is clear from the condition of the young Notidanid; and in the absence of further embryological data I can only conclude that the *Batoidei* do present us with the least modified condition of the parts, and that the duct-like base of the appendix digitiformis seen in them is the representative of a structure closely comparable to, if not homologous with, the cæcum coli. Whether that portion of this "duct" which, in the *Selachoidei*, skirts the wall of the gut is a superadded passage formed from behind by a duplicature of the mucous membrane, as Blanchard supposes (2. p. 182), has yet to be proved; from the facts herein recorded, I incline to the belief that it is not, but that the apparent superaddition may have resulted from adhesion.

The processus digitiformis is, as Duméril has remarked (7. p. 158), "a true secretory organ." Its secretory glands have been compared by Leydig (21. p. 57) to those of Brunner, met with in the mammalian intestinal wall; and he calls attention to the "dirty yellow" nature of their product. Blanchard has attempted to institute (2. p. 181) comparisons between the secre-

* That alluded to by him in P. Z. S. 1876, p. 44.

tion of this gland * and that of the "anal or circum-anal glands of many higher animals;" and he accordingly proposes to term it the "*glandula superanalis*" (*l. c.* p. 182). To English students this structure is best known as the "rectal gland." Blanchard's researches seem to point to its origin as an outgrowth of the hypoblastic gut; those structures which we commonly term "rectal" or "anal" glands, are associated with the terminal epidermal portion of the hind gut, and it is tolerably safe to conclude that from this they are developed. Proof that this is so does not appear to be at present forthcoming; but the facts to which I have alluded warrant the withdrawal of the term "rectal gland" in the case of the *Plagiostomi*.

The appendix digitiformis has been by Hyrtl regarded (**18.** pp. 28–29) as accessory to the reproductive apparatus rather than to the alimentary. He based his assumption † upon the failure to find food-stuff within it, and upon a belief in its increase in size in animals whose oviducts contained eggs. I have examined a series of specimens of *Raia* and *Mustelus* having eggs and young in their oviducts, in vain, for confirmation of Hyrtl's belief; and confidence in the same is further shaken by the fact that his views fail to explain the presence of the organ in the male in a form indistinguishable from that of the female. Moreover, the course taken by its duct, and the fact that its secretion is discharged well forwards into the intestine, would appear to be irreconcilable with this view. In the fact that this organ is a secretory one, we have, in the long run, a further point of agreement with the cæcum coli and appendix vermiformis. The fact that the latter becomes an adenoid in its most highly differentiated form, while the processus digitiformis is not known to be thus constituted ‡, would appear to be of minor significance, by analogy with Weldon's discovery (**32.** p. 176) that

* On p. 181 of his pamphlet, Blanchard attributes to Milne-Edwards (Anat. et Phys. Comp. t. vii. pp. 326, 332) the belief that this structure represents "a special urinary bladder." M. Milne-Edwards makes ("in seinem trefflichen Lehrbuch" [Blanchard, *l. c.*]) no such statement; he alludes not to the appendix digitiformis, but to the well-known urinary receptacle, which I have elsewhere proposed to term the Wolffian bladder (Journ. Anat. & Phys. vol. xxiv. [n. s. vol. iv.] p. 408, 1890).

† Blanchard (*l. c.*) appears to have been unaware of this.

‡ Migratory leucocytes have been observed in the "cloacal epithelium" of *Raia*, *Torpedo*, and *Squatina* (List, J. H., "Studien an Epithelien," Archiv f. mikr. Anat. Bd. xxv. pp. 264-268, 1885).

the supra-renal body in the Ichthyopsida (*Bdellostoma*) probably represents a metamorphosed excretory blastema.

I trust to have shown in the foregoing that the appendix digitiformis and its related conduit correspond, in fundamental relationship, with the appendix vermiformis and cæcum coli; and I think it not improbable that in the former, as represented in the *Batoidei* (*cf. ante*, p. 398), we may be dealing with the latter in their original form. It is a curious fact that Monro, in his classical work on Fishes, referred to the appendix digitiformis on one page (**23.** p. 84) as the "appendix vermiformis" and on another (p. 92) as the "cæcum;" while Wiedersheim, commenting (**33.** p. 565) on the size and character of the cæcum coli of *Amphisbæna* *, has incidentally likened it to the appendix digitiformis of the Selachii. I would go further, and openly declare a belief in homology between the two sets of structures as defined by myself (p. 394) until proof to the contrary, more conclusive than that which is at present forthcoming †, shall have been brought forward.

IV. *On the Cæcum of the Teleostei.*

It is customary in text-books to deny the existence of a cæcum among the Teleostean fishes. Such an organ was, however, accorded them by Home in 1814 (*Scorpæna* [**15.** p. 389, **16.** pl. xcii.]); Rathke, ten years later, described ‡ a cæcum in *Cyclopterus* ("See Hase") and *Trigla lyra*, while Cuvier and Valenciennes accredited the same (**5.** p. 354) to *Box* in 1830.

* On examination of this in *Lepidosternon*, *Blanus*, *Pachycalamus*, and *Amphisbæna* (*alba*, *fuliginosa*, and *darwinii*), I fail to see anything much in advance of the ordinary Lacertilian type.

† The danger of drawing comparisons from the histological structure of the alimentary mucous membrane alone is greatly increased by the discovery of thickly set Peyer's patches in the large intestine and rectum among Rodents, Insectivores (Dobson, Journ. Anat. & Phys. vol. xviii. pp. 388-392, 1884), and Apes (*Hapalemur*, Beddard, P. Z. S. 1884, p. 395). A similar caution is necessitated by Weber's description of racemose sudoriferous glands in the *Hippopotamus* ("Studien über Säugethiere," Ein Beitrag zur Frage u. d. Ursprung d. Cetaceen, pp. 14–18, Jena, 1886).

‡ **29.** pp. 80, 81. He also attributed to *Polypterus* a cæcum, with the comment "wen ich mich richt erinnere." There can now be little doubt that Joh. Müller was right in subsequently regarding this ('Bau u. Grenzen der Ganoiden,' p. 23) as a pyloric cæcum; for, among Teleostei, the cæca pylori may be reduced (*Ammodytes*, *cf.* Rathke, **29.** p. 87) to a single representative.

The terminal portion of the intestine in these fishes exhibits, as a general rule, an increase in calibre and distensibility over the rest, and at its point of differentiation there is usually present, in the adult, a well-defined valve (*cf.* Cuvier and Valenciennes, 4. p. 502) which clearly suggests the ileo-colic valve * of the higher Vertebrata.

The cæcal diverticulum, when present, overhangs this; and, although it never attains a considerable development, comparison with the other Ichthyopsida and the Reptilia leaves little room for doubting that it represents those derivatives of the gut which I have attempted to homologize in the preceding part of this paper. Having accumulated some notes upon the same in those genera before referred to which I have been able to examine, I here tender them for what they may be worth.

Trigla gurnardus. The ileo-colic valve is, in the adult, exceedingly well marked—so much so that it reduces the ileo-colic aperture to a minute perforation. The large intestine exhibits but a small increase in calibre as compared with the ileum; and there is consequently no trace, in the adult of this species, of an overhanging lobe or cæcum. I have observed, however, in a young specimen of $16\frac{1}{2}$ centim. in length, a perceptible enlargement of the antero-dorsal extremity of this viscus, suggestive of the small cæcum of the Frog (*dv'*, fig. 3).

Cyclopterus lumpus. I am unable to confirm Rathke's statement concerning the presence of a cæcum in the adult of this species. The ileum enters the large intestine antero-ventrally (*cf.* Pl. II. fig. 17); the increase in calibre of the latter is well marked, and there is developed a highly efficient and flap-like ileo-colic valve. In the young animal, however, the conditions may be otherwise. I have examined two juveniles of this species †. The intestine appeared, in them, when looked at externally, to be destitute of a cæcum; when opened from the side, care being taken to avoid unnecessary displacement of the gut, the ileo-colic aperture was seen to be situated ventrally (fig. 17) and, in one of the two, comparatively far back. The ileo-colic valve

* It is very regrettable that this should be so frequently referred to, alike in original monographs and text-books of both anatomy and physiology, as the ileo-cæcal valve. Huxley has long since shown this term to be expressive of an error of observation in fundamentals (see Parker, P. Z. S. 1881, p. 625).

† Thanks to Prof. W. McIntosh, F.R.S., and my pupil Mr. E. W. L. Holt.

was represented by the tumid and inpushed base of the ileum, and from that it would appear to be, in all probability, derived. A line drawn vertically through the same (a—β of fig. 17, Pl. II.) passes behind an overhanging lobe of the large intestine—the cæcum (*dv'*). Curiously enough no such enlargement was to be seen in the second specimen; and the question naturally arises whether, after all, the differences between it and the other one may not have been due either to over-distension in the one case or over-contraction in the other. Further investigation can alone settle this matter; but it is interesting to point out that a precisely similar difficulty arises in relation to the alleged discovery, by Perrault*, of a cæcum in *Salamandra*.

Box vulgaris†. Cuvier and Valenciennes state of the intestine of this fish (5. p. 354) "arrivé dans la partie moyenne du ventre, il se dilate subitement et donne même une sorte du petit cæcum très-court à l'origine du rectum, qui se rétrécit bientôt et se rend à l'anus." This "cæcum" is, in this fish, unmistakable and well marked externally, and it lies to the left side (*dv'*, fig. 16). The stomach of this species is remarkable for the characters of its pyloric sac; that (*st''*, fig. 17) instead of being short and swollen, as is so generally the case among the Teleostei, is elongated and tubular. The cardiac gastric sac (*st'.*) is constricted at its middle and, with the base of the stomach, prolonged back into a crescentric diverticulum, into the concave border of which the head of the large intestine (*i.l.*) is received. On dissection of this fish from the side, the air-bladder is seen to be greatly enlarged; its posterior moiety tapers off much less suddenly than usual, and it, together with the greatly developed fat masses, obliterates for the most part the posterior two thirds of the cœlom. The cæcum, when examined with sufficient care, is seen to be situated dorso-laterally rather than laterally, and to occupy a position which points very strongly to the conclusion that it and the immediately related intestinal wall have undergone a displacement (in mutual adaptation to the surrounding organs) of a precisely similar nature to that affecting

* 'Mém. pour servir à l'hist. nat. des Animaux,' 3e partie, pl. 16, p. 481. (*Cf.* Milne-Edwards, Leçons s. l. Phys. et l'Anat. Comp. t. vi. p. 354.)

† I have to thank Dr. Günther, F.R.S., for a well-preserved specimen of this fish.

Cuvier and Valenciennes describe (5. p. 364) two cæca in *B. salpa*. I regret having been unable to procure an individual of this species.

the cæcum coli and appendix digitiformis of certain other Vertebrata (cf. *ante*, p. 396).

An ileo-colic valve is not differentiated.

It may be urged, against my belief in an homology between the above-described cæcum of the Teleostei and the cæcum coli of the higher Vertebrata, that the intestinal (*ileo-colic*) valve of the former appears to lie within the area of the so-called spiral valve of the Clupeoid *Chirocentrus* * and of the annulations of the intestinal mucous membrane in the Salmonidæ and other Teleostei (*cf.* Rathke, 29. pp. 62 *et seq.*). In *Chirocentrus* the prevalvular gut is short, and the intestine passes to the exterior without convolution. In the Salmonidæ the prevalvular gut is elongated and bent upon itself. Huxley, writing on this subject, says (*l. c.* p. 138):—"I am inclined to believe that the circular valve which separates the colon from the rectum in the Smelt is merely a last remainder of the spiral valve" (of the Ganoids and *Chirocentrus*). This valve occupies in the Smelt precisely the position of that which I have been led to compare (*ante*, p. 401), in other Teleostei alluded to, with the ileo-colic valve of the higher Vertebrata. Assuming, for the moment, that the annulated segment of the gut in the Trout and Salmon and the post-valvular portion in the Smelt are homologous, and representative of the large intestine of other Teleostei, examination of these in the order named might, at first sight, appear to show evidence of a gradual diminution in length in passing from the former to the latter. Rathke, six-and-thirty years ago, drew attention (*l. c.*) to the fact that in the Salmonidæ the annular folds alluded to are susceptible to great variation and difference with age. He, nevertheless, regarded them as restricted to the rectum. If the lining membrane of the Smelt's intestine be carefully examined it will be found to be produced into a very obvious series of crenulated annular folds, throughout the area occupied by the more definite series of the Salmon and Trout. The valve to which Huxley alludes, and which I regard as the probable homologue of the ileo-colic valve, lies within an interrupted area in this series—in the Salmon and Trout it is absent.

* Cuvier and Valenciennes, 'Hist. nat. des Poissons,' t. xix. p. 151, pl. 565. *Cf.* Huxley, P. Z. S. 1883, p. 138.

In view of the constancy of this valve, and of its relationships previously referred to, as compared with the variability of the annular folds, I am decidedly of opinion that, if the homology between the latter in the Smelt and Salmonidæ named be admitted, that segment of the gut which bears them must represent something more than the large intestine, as I have defined it—whereupon the post-valvular portion of the Smelt's intestine and the annulated segment of that of the Salmon and Trout would appear to be non-homologous. In face of these facts and considerations, the conditions in *Chirocentrus* become most perplexing. On comparison with the Elasmobranchs, its valved intestine might represent that which I regard, in them, as the small intestine—in which case the large intestine would appear to be absent and the gut, taken as a whole, to be less modified than that of even the Ganoids. On the other hand, comparison with the Salmon would appear to show (if the annulated segment of the gut of that fish should have the value which Rathke attached to it) that the valved gut in *Chirocentrus* might represent the large intestine as defined by myself.

That, in seeking to establish homologies, too much importance must not be attached to the mere presence or absence of an intestinal spiral valve in the Teleostei, is clear, from the differentiation of a like structure in the œsophagus of *Chanos* *, and of an essentially similar one in that of the *Marsipobranchii* †. I have attempted to show (*ante*, p. 395) that the large intestine is, in the Plagiostomes, well marked though short. The appendix digitiformis is smallest where situated furthest back; and in the young of those forms which I have been able to examine (*Scyllium*, *Mustelus*, *Acanthias*, *Heptanchus*) it is situated further forwards than in the adult. We have thus a suggestion of reduction proportionate to a shortening up of that which I regard as the large intestine; a further extension of such a process (be it at work) would give us the condition met with in the Ganoids and *Chirocentrus* (supposing the resemblances between the intestine of this fish and that of the Plagiostomes to

* Cuvier and Valenciennes (**6.** p. 185).

† Günther describes this ('Introduction to the Study of Fishes,' p. 128) as consisting of "numerous longitudinal folds." They are oblique and more nearly ovoidal. Parker has shown (**26**) that the particular characters in the "pitch" and mode of disposition of such "valves" are matters of no morphological significance (*cf.* his pl. 10. figs. 1 and 4, and pl. 11. figs. 6 and 8).

be indicative of homological relationship); the converse process would tend towards that of the majority of the Teleostei and of the higher Ichthyopsida*.

If this comparison should stand the test of future investigation, the folds of the intestinal mucous membrane in *Chirocentrus* and the *Salmonidæ* will be non-homologous. To deny that the large intestine of the majority of the Teleostei, as herein defined, represents that of the higher Vertebrata, would be, in the present state of our knowledge, to imply that the comparative method upon which our fundamental conceptions in morphology are based is untrustworthy.

The large intestine remains comparatively short throughout the Ichthyopsida, the Sauropsida, and the lower Mammalia; it is not until an ascending term in the Mammalian series is reached that it shows signs of clear differentiation into the colon and rectum so well known among the higher representatives of the same. That the cæcum coli, however, not only

* Owen and Hyrtl have long ago described in *Protopterus* a median diverticulum of the antero-dorsal wall of the cloaca, believed by them to represent the urinary bladder. Parker has recently overthrown their interpretation, and proposed (**28.** p. 14) to term the organ the *cæcum cloacæ*—comparing it with the Plagiostome's appendix digitiformis; his proposal receives a special interest from the fact that Günther has described the appendix digitiformis of *Chlamydoselache* (**11.** p. 3) as "a globular glandular body of the size of a large pea," which "lies dorsad of the cloaca, into which it discharges its secretion by a short duct"—a condition unknown in any other Plagiostome. Garman, on the other hand, speaks of it (**10.** p. 20) as "a cæcal pouch behind the (spiral) valve."

I am indebted to my friend Mr. G. A. Boulenger for the opportunity of examining the parts in question in this Japanese Shark. Dr. Günther does not state exactly in what sense he uses the term "cloaca"; if by this we are to understand that portion of the gut situated posteriorly to the anal and urino-genital orifices, Garman's description in perfectly correct. The duct of the processus digitiformis is short and, like that of other Selachii, forwardly directed; it opens but a short distance in front of the anus and much nearer the same than in any other Plagiostome which I have examined. The whole condition of the parts related favours the belief in the shortening up of the large intestine arrived at above, and that is strengthened by the insignificant size of the cloaca, which would appear to have been involved in the process.

Parker's cæcum cloacæ opens directly backwards by a wide aperture; it is present in both sexes, and it might conceivably represent the conduit at least of the Batoid processus digitiformis (*dv'*, fig. 1) in a much modified form. It appears to me, however, to most nearly recall that diverticulum in the female Chimæroid which Hyrtl termed (Sitzb. Wien. Akad. Bd. xi. 1853, pp. 1085–86) the "*vesicula seminalis*," and the absence of a corresponding vesicle in

exists in the class Pisces, but is present, in a low order of the same, in that which may probably prove to be its original form, I fully believe. Moreover, the facts go to show that in certain Teleostei (*Trigla*, *Cyclopterus*) the small cæcum may possibly disappear as the intestine increases in convolution; and it therefore becomes a matter of interest to inquire whether the first-named structure may not be more generally represented in at least the young of that order.

V. *In Conclusion.*

The deductions which I have drawn are based chiefly upon facts arising out of a comparison of leading blood-vessels; and I fully anticipate that it will be doubted whether these are to be trusted, to the extent claimed, as guides to homology. Precedent might be cited to suggest that they are not—the recent investigations of Boas (3) and Zimmermann (34) into the aortic arches, of Hochstetter (12) into the post-caval and azygos veins, and of Parker (27) into the lateral epigastric veins, justify the belief that they are. Objections may be here raised on the ground that the great vessels just named do not undergo variation such as do those of the intestinal series upon which I am relying. Against this there must be set the fact (which, so far as I can ascertain, has escaped notice) that the fifth aortic arch, which Boas has so successfully shown (3 *et op. cit.*) to be present between the aorta and the pulmonary artery of the Urodeles, may be (*Salamandra*) either absent on one or both sides or, when present, variable between the condition of a widely open tube and that of a vestigial cord of insignificant proportions.

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the male Chimæroid is an obstacle in the way of a belief in its homology with the processus digitiformis of the Plagiostome.

Günther has described (Phil. Trans. 1871, part ii. pp. 546–47) the genital ducts of *Ceratodus* as opening, together with the ureters, into a "urinal cloaca;" and the latter would appear, at first sight, to answer to the cæcum cloacæ of *Protopterus*. I have not been able to examine the male *Ceratodus*, but I think it tolerably certain, on examination of the female, that Parker's "cæcum cloacæ" and Günther's "urinal cloaca" will prove to be distinct in origin, and that the latter will be found to represent that portion of the Elasmobranch's cloaca which I herein term (*ante*, p. 383) the "oviducal recess" (*cl'''*, Pl. I. fig. 1). Indeed this has been, in a sense, already anticipated by Günther, who refers to the sac on one page (*l. c.* p. 546) as "a dorsal diverticle of the rectum," and on the next (p. 547), in somewhat contradictory terms, as "the cloacal dilatation."

There is indicated in the concluding sentence of the preceding section one of the next steps in this inquiry; others lead to a further investigation into the histology and development of the appendix digitiformis, and to a study of the comparative histology of those structures to which the terms "cæcum coli" and "appendix vermiformis" have been applied. Upon these I propose to enter on a future occasion.

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VII. EXPLANATION OF THE PLATES.

Figs. 1, 3, 4, 5, and 6, and figs. 7, i. to v. are drawn to the same scale in order to facilitate comparison; the dorsal aorta (*ao.*) is, in all but 7, iii. iv. & v., delineated up to the point of origin of the iliac arteries. Only vessels of the precaudal median-intestinal series are indicated; all others are intentionally omitted.

Figs. 8 to 14 are drawn to the same natural size, proportionate to the transverse diameter of the base of the valved intestine.

Plate I.

Fig. 1. *Raia clavata*, adult ♀. The cloaca and terminal portion of the intestinal canal, with related arteries, dissected from the side, after injection with French blue. $\frac{3}{4}$ nat. size.

2. *R. clavata*. To show the origin and relationships of the paired cloacal arteries. $\frac{3}{4}$ nat. size.

3. *Rana temporaria*, ♀. A similar dissection to fig. 1. The arteries represented are a combination of those observed for four individuals referred to in the text. × 2.

4. *Rana temporaria*, ♂. To show the base of the inferior mesenteric artery, in an individual specimen described in the text. × 2.

5. *Salamandra maculosa*, ♀. Comparison dissection to figs. 1 & 3. × 2.

6. *Salamandra maculosa*, ♂, showing two inferior mesenteric trunks. × 2.

7. To represent the dorsal aorta and the origin of the cœliac and mesenteric arteries in relation to the same in—i. *Salamandra maculosa*; ii. *Raia clavata*; iii. *Mustelus antarcticus* (after Parker [27]); iv. *Scyllium canicula*; v. *Acanthias vulgaris*.

Plate II.

Fig. 8. The appendix digitiformis, with its related parts, in median longitudinal section, in *Zygæna malleus*.

9. The same, in *Raia clavata*.

10. The same, in *Læmargus borealis*.

11. The same, in *Scyllium canicula*.

12. The same, in *Cestracion philippi*.

13. The same, in *Acanthias vulgaris*.

14. The same, together with a portion of the valved intestine, in *Notidanus* (*Heptanchus*) *cinereus*.

15. The same, in *Rhina squatina*; external view. Nat. size.

16. The cæcum and adjacent portions of the alimentary viscera, in *Box vulgaris*. × 2.

17. The head of the large intestine of *Cyclopterus lumpus* (juv.), as seen from the right side. × 2.

Reference letters.

a.c. Cœliac artery.
a.cd. Caudal artery.
a.cm. Cœliaco-mesenteric artery.
a.g. Genital (ovarian) arteries.
a.i. Iliac arteries.
a.im. Inferior mesenteric arteries.
ao. Dorsal aorta.

a.r. Posterior renal arteries.
bl'. Allantoic bladder.
bl''. Orifice of the same.
cl'. Cloaca.
cl''. Epidermal portion of the same.
cl'''. Oviducal recess of the same.
dv'. Cæcum coli (or its probable homologue).
dv''. Appendix digitiformis.
f. Longitudinal fold in roof of large intestine.
i.l. Large intestine.
i.s. Small intestine.
od'. Left oviduct.
od''. Right oviduct.
p. Pelvic girdle.
st'. Stomach, cardiac sac.
st''. Stomach, pyloric sac.
v.i. Intestinal (spiral) valve.
v.ic. Ileo-colic valve.

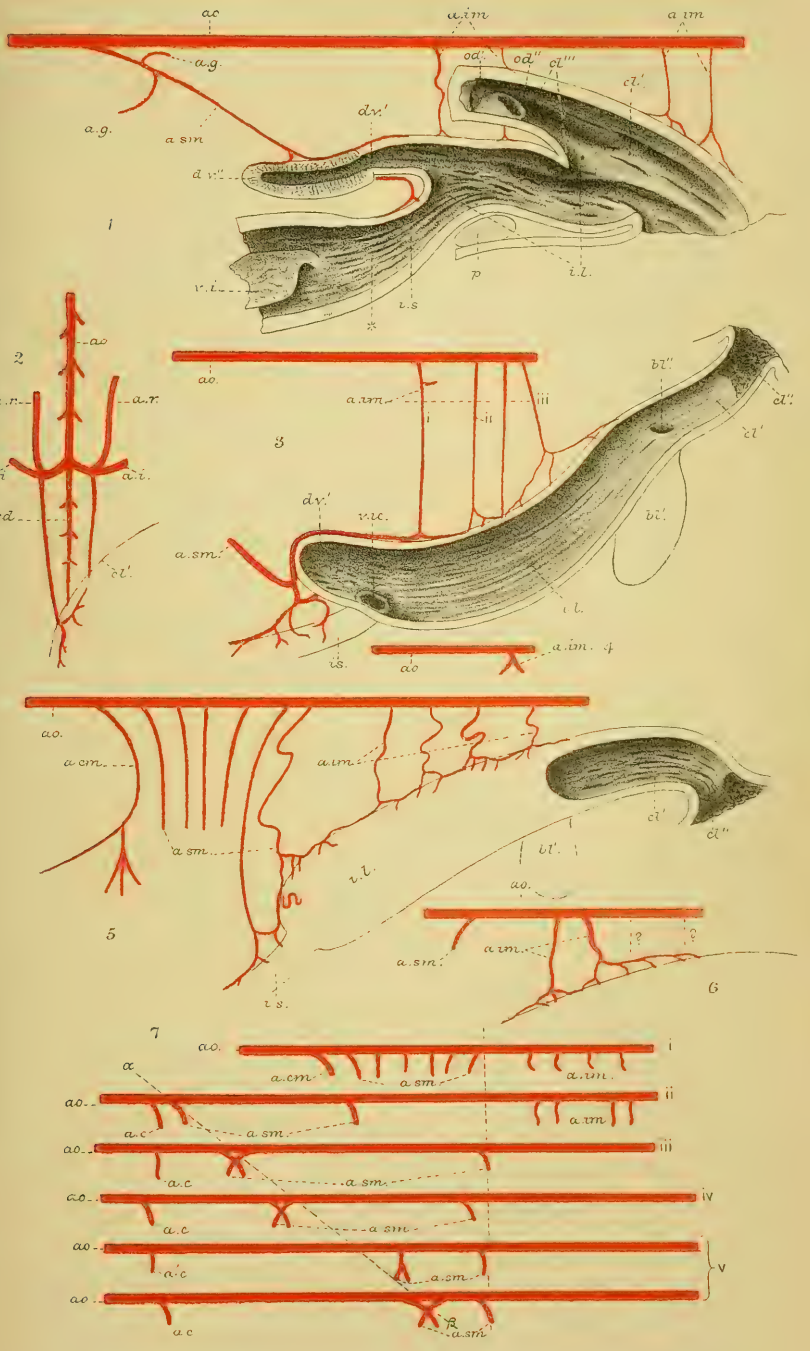
On the Tongues of the British Hymenoptera Anthophila.

By Edward Saunders, F.L.S., F.E.S.

[Read 17th April, 1890.]

(Plates III.–X.)

In Vol. XVII. of this Journal Mr. Travers J. Briant has ably described the tongue of *Apis mellifica* and its anatomy, and I purpose in this paper to give descriptions of this organ in other British genera of Hymenoptera Anthophila, accompanied with figures carefully drawn from slides prepared by Mr. Enock, whose skill in this direction is well known. At the present time I know of no figures that, in any way, give an idea of the beauty and complexity of structure which characterize the different genera. The number and proportionate lengths of the joints of the palpi and the general form of the so-called lingua have been the only characters usually selected for generic determination, whereas the form of the *lora*, *submentum*, *scales of the maxillæ*, and *paraglossæ* afford additional characters quite as important, as will be seen by the accompanying Plates. As a general result from the study of these organs, it would appear that there is a gradual modification of form from the short bifid



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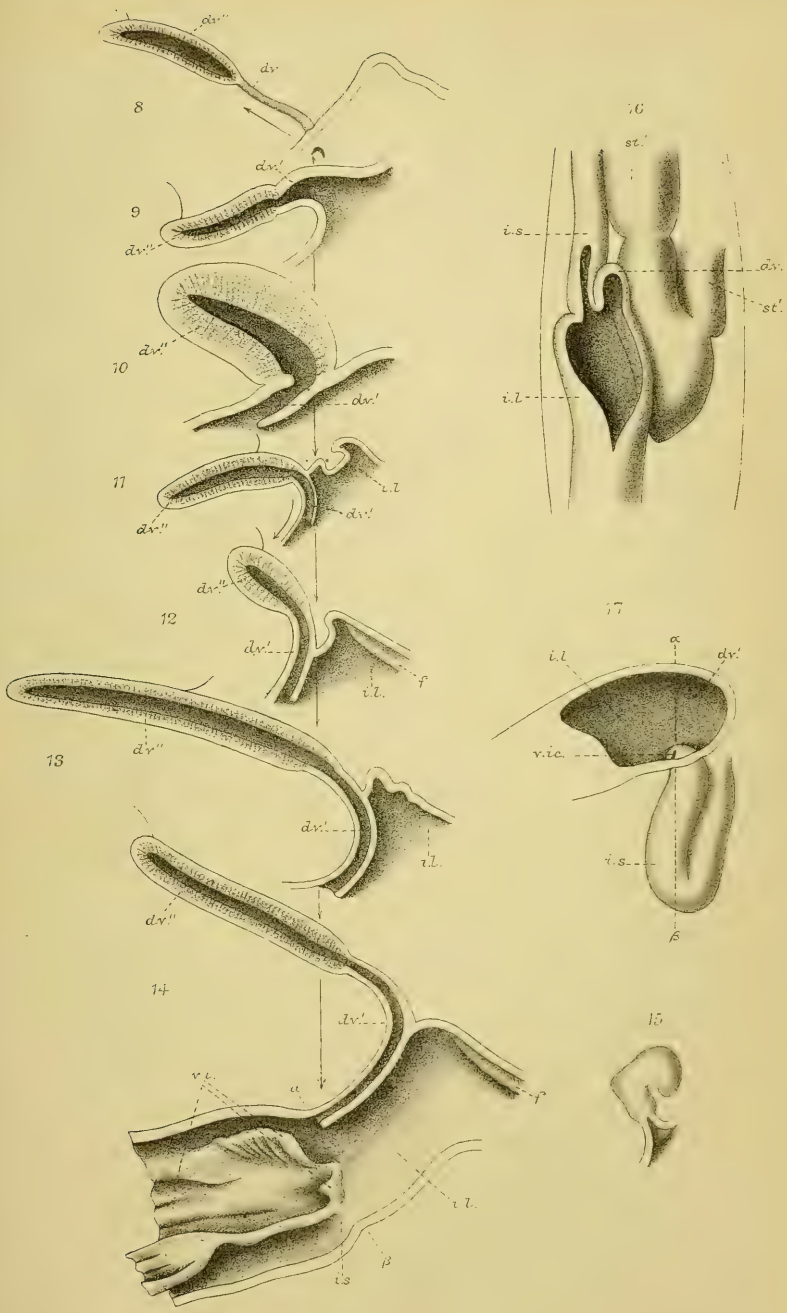
Intestinal Canal & Arteries of Ichthyopsida.



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